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A STATISTICAL TEST OF THE SPECIES CONCEPT IN LITTORINA

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"One may believe that if larger series were more often utilised in taxonomic work the current bewilderment over variation would give way to a renewed respect for a certain uniformity that exists thruout such groups of individuals."—Kinsey.

With certain exceptions, no two individuals of a species are ever genetically identical; hence it is not so much the uniformity as the character and range of variation in a species that are diagnostic. Conversely, the fact that two related animals differ does not necessarily mean that they belong to separate species unless it can be shown, after the examination of sufficient numbers collected over a wide area, that there is not a series of overlapping intergrades between the two differing forms.

It was, for example, the range in variation in the number of vertebræ in conger eels that enabled Johannes Schmidt (1931) to separate the American species, *Conger oceanicus*, from the European *C. vulgaris*. The ranges of the larvæ of the two species overlap in part geographically, but not anatomically, the number of vertebræ in *C. oceanicus* being from 140 to 149, average 144.63, and in *C. vulgaris* from 154 to 163, average 158.16. This lack of overlap in the numbers of their vertebræ clearly justifies their segregation.

Kinsey (1930) has shown, too, that the highly variable Gall Wasp, *Cynips erinaceus*, is one species, though extreme forms of its gall have been previously assigned to separate species. In any part of its wide range a comprehensive collection over a square mile will very closely resemble a similar comprehensive collection at any other place in the insect's range. The variation in the species is roughly constant throughout its entire geographic range.

These are two extreme cases; the first of two distinct, the second of one homogeneous, species. If, however, the two conger eels had

numbers of vertebræ ranging from 140 to 152 and from 150 to 163 respectively, it would be impossible from the vertebræ alone to assign to either group those possessing 150, 151 or 152 vertebræ. To get round this difficulty, one man would consider them mere races, another sub-species, and a third separate species with a certain amount of hybridization, the choice depending on the taxonomic upbringing and prejudices of the worker.

Again, if in such a case as *Cynips erinaceus* the amount of variation were not constant, a comprehensive collection from one part of its range would be different from a similar collection from another part. If the variations in these two collections did not overlap, they might be considered separate species unless they were merely the ends of a continuous series.

This last is the case with *Littorina obtusata*. There has been but little uniformity in the treatment of its varying forms, and the resulting taxonomic muddle must be first of all cleared up.

The establishment of the genus *Littorina* has always been ascribed to the elder Férussac, the reference in the Index Animalium (Sherborn, 1927) being to page xxxiv of the Tableaux systématiques généraux de l'embranchement des Mollusques (Férussac, 1822). This refers, however, only to where *Littorina* is listed as the fifth sub-genus of the genus "PALUDINE, Paludina, FÉRUSS. (Fluv. et marin.)," with no definition or description. The definition, such as it is, is given on page xi, where Férussac says: "Quant aux paludines marines qui constituent le genre Trochus d'Adanson, comme nous n'avons pu adopter cette dénomination à cause des *trochus* de Linné (en general formés d'espèces réellement congénères, ce qui nous a empêché de les appeler *turbo* avec Adanson, en y rapportant tous les *turbo* de Linné qui doivent s'en rapprocher), nous en formons un sous-genre sous le nom de *littorine*." (No Latin is used here, but an objection on that score would, I think, be oversteeped in pedantry, since only the final *e* needs altering.) Two pages before, at the bottom of page ix, Férussac gives a list "dressé d'aprés l'édition de Gmelin," referring to the thirteenth edition of the Systema Naturæ, edited by J. F. Gmelin (Linnæus, 1788). This list, compiled from the Linnæan genera *Trochus* and *Turbo*, which Férussac wished to combine, includes five species referred to as "*Paludina* Marine." These are *obtusatus*, *neritoides*, *littoreus*, *muricatus*, and *afer*, constituting his sub-genus *Littorina*.

"Le genre Trochus d'Adanson," mentioned above, consists of four species described and illustrated in the Histoire Naturelle du Sénégal (Adanson, 1757). Their names, on a binomial system of Adanson's

own devising, antedate the tenth edition of the Systema Naturæ (Linnæus, 1758) by one year, and therefore do not stand. These species are beautifully illustrated in Adanson's work, and undoubtedly belong to the genus *Littorina*.

Menke, 1828, was responsible for the spellings *Litorina* and *litorea*, although both Linnæus and Férussac used two *t*'s. Menke said that the alteration made for correct Latin, which is true, but it also led to a small confusion in nomenclature which has lasted till this day. In truth, "optima nomina quæ nihil significant."

The first full definition or description of the genus *Littorina* is given in the second edition of Lamarck's Histoire Naturelle des Animaux sans Vertèbres, Vol. XI, pp. 201 et seq. (Lamarck, 1843).

Of the British Littorinas, *L. littorea* and *L. neritoides* are both described under the genus *Turbo* in the tenth (1758) edition of Linnæus' Systema Naturæ, and they have retained their original specific names and authority, except in the work of a few authors who have fortunately caused no lasting confusion, save for the fashion, introduced by Menke (1828), of spelling with one *t*.

The nomenclature of the mollusks generally known by naturalists as *L. obtusata* and *L. rudis*, however, has for a long time been a field for error and dispute.

Littorina rudis is assigned by the Marine Biological Association (1931) to Maton, quoting Jeffreys (1865). Johnson (1915) gives *L. rudis* (Donovan), quoting Gould (1870) and Donovan (1804) (whose date is erroneously given in Gould as 1800, the date of publication of the second volume; the first volume was actually published last, in 1804, after the fifth in 1803). Kuester (1856) calls the unfortunate animal *L. rudis* (Montagu), quoting Montagu (1803) and Maton and Rackett (1807), in spite of the fact that the latter authorities cite Maton (1797) as the originator of the name and description; Jeffreys (1865) also gives Maton. Forbes and Hanley (1853), however, mention Donovan (1804), though Maton and Rackett (1807) give Maton (1797), Montagu (1803) and Donovan (1804) in order of priority. Montagu disturbs this order by quoting from the then unpublished volume of Donovan, having presumably seen the manuscript or proofs, but Donovan nevertheless gives the credit of the name *rudis* to Maton (1797). Menke (1830), the first to put *Turbo rudis* into the genus *Littorina*, cites Montagu (1803) as author of the species.

Under the Law of Priority, the name *rudis* must be referred to Maton (1797), since there is no doubt of the identity of the form he described.

However, *rudis* is not the correct specific cognomen of the snail which usually passes under that name. In 1792 Olivi published a description and rough figures of a shell near Venice which he called *Turbo saxatilis*. Jeffreys (1865) states that this form is identical with *Littorina neritoides* (L.), but Dautzenburg and Fischer (1912) present on two plates sixty-two exquisitely colored and enlarged figures of *L. saxatilis* and *L. rudis*, which show that *L. rudis* is specifically indistinguishable from *L. saxatilis*, of which names the latter has the priority by five years (1792 and 1797).[1]

In the case of the snail variously known as *Littorina obtusata*, *L. littoralis* and *L. palliata*, the difficulties begin with the tenth edition of the Systema, where two very similar shells are described under different genera, to wit, *Turbo obtusatus* (Vol. I, p. 761) and *Nerita littoralis* (Vol. I, p. 777). The early British conchologists Montagu (1803), Donovan (1804) and Maton and Rackett (1807) all accepted *Nerita littoralis* as representing the common form of the English Channel and British Coasts. Here Montagu introduces a minor confusion by claiming that *Nerita littoralis* L. is the same as *Turbo neritoides* L. He is alone in this opinion, and it is difficult to see what led him to form it. In 1822 Thomas Say described *Turbo palliatus* from the coast of Maine, and this is considered by both Dautzenburg and Fischer (1915) and Johnson (1915) to be a variety or sub-species of the *Turbo obtusatus* of Linnæus.

Jeffreys (1865) gave the specific name *obtusata* to the form on the shores of the English Channel, evidently assuming the identity of the two Linnæan shells. Dautzenburg and Fischer (1915) regard the English Channel (*littoralis*), the Norwegian (*obtusata*) and the New England (*palliata*) forms as varieties or subspecies of the one species, of which the prior name, by pagination in the Systema Naturæ, must be *Littorina obtusata*. Winckworth (1922), however, assigning the British Littorinas to four genera,[2] *Littorina* Férussac, *Littorivaga* Dall, *Melarhaphe* Menke and *Neritoides* Brown, includes in the last-named the three species *obtusata* (L.), *æstuarii* (Jeffreys) and *littoralis* (L.), the existence of *obtusata* on the shores of Great Britain being thought

[1] *L. saxatilis* (Olivi) is not to be confused with *L. saxatilis* (Johnston), which is a so-called variety from Berwick, England (Jeffreys, 1865).

[2] These generic names are regarded in this paper as only of subgeneric rank. They are extremely valuable in the finer delimitation of the genus *Littorina* as a whole, but considered as genera they only bewilder the poor naturalist and field worker.

Very full lists of synomymies are given for the *obtusata-littoralis-palliata* group by Dautzenburg and Fischer (1915) and for *saxatilis-rudis* by Dautzenburg and Fischer (1912).

doubtful, all of which leads us to the impasse of a difference of opinion among experts.

This confusion is due solely to the fact that inferences about varieties have been drawn from individual specimens, and the only way to unravel this tangle is to examine a large enough number of animals until the answer to the problem ceases to be a matter of opinion.

Specimens of *L. obtusata* were therefore obtained from eleven different localities, on both sides of the Atlantic Ocean. The minimum number aimed at was one hundred from each locality, but sufficient

TABLE I

Localities, number of individuals and catalogue numbers of eleven lots of L. obtusata.
M.C.Z. = Museum of Comparative Zoology, Harvard University.
B.S.N.H. = Museum of Boston Society of Natural History.

	Locality	No.	M.C.Z.	B.S.N.H.
a..	Bergen, Norway	100	47508	
b..	Cattewater, Plymouth, England	100	76980	
c..	Church Reef, near Plymouth, England	100	76978	
d..	Near Westerly, Rhode Island	100	13980	
e..	South Cohasset, Massachusetts	100		26655
f..	Briar Neck, Gloucester, Massachusetts	86		24787
g..	Rye Beach, New Hampshire	75		26806
h..	Broad Cove, Georges River, Cushing, Maine	38	67775	
i..	Port Clyde, Knox County, Maine	74	67773	
j..	Tenants Harbour, Knox County, Maine	60	67774	
k..	Isle au Haut, Maine	100	13972	
	Total	933		

specimens were not always forthcoming. In only one case, however, was the number less than sixty. Table I gives the localities of the lots, the number of individuals, and the catalogue numbers in either the Museum of Comparative Zoölogy, Harvard University, or the Museum of the Boston Society of Natural History.

The positions of the localities are shown in the maps, Figs. 1 and 2.

The lot *a* in Table I were kindly sent to me by Professor Brinkmann of the Bergens Museum, lots *b* and *c* by the Marine Biological Association at Plymouth, England, lots *i* and *j* by Mr. N. W. Lermond, and lots *e*, *f* and *g* were lent by Mr. C. W. Johnson of the Boston Society of Natural History. The rest, *d*, *h*, and *k*, were already in the collection of Harvard University.

Each shell was measured with callipers to the nearest tenth of a millimeter along three dimensions; the length (*a*) of the final whorl

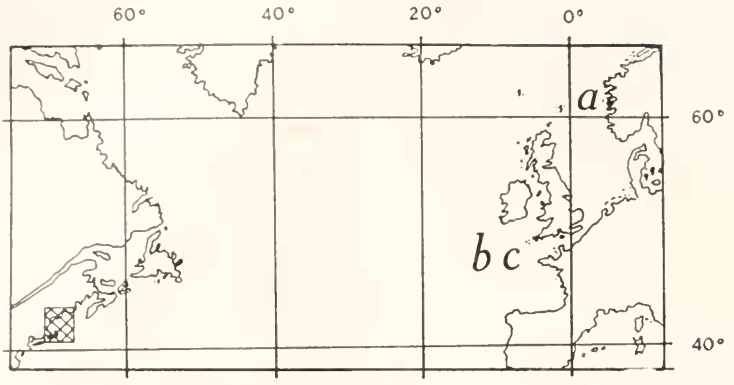

FIG. 1. Map showing the localities on the two sides of the North Atlantic. The shaded area is that shown on a larger scale in Fig. 2. The letters refer to Table I.

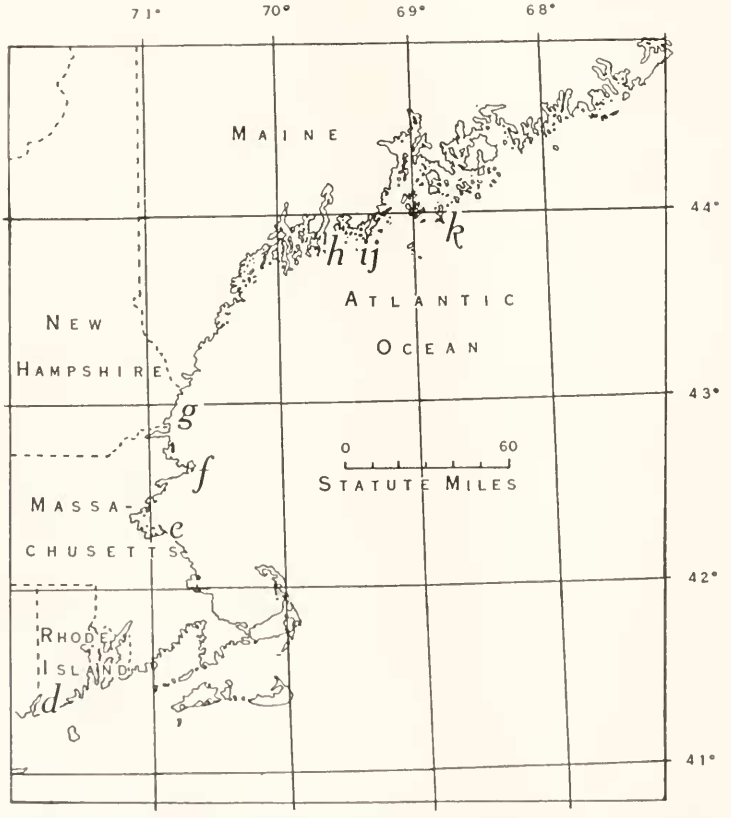

FIG. 2. Map showing the localities on the New England Coast. The letters refer to Table I.

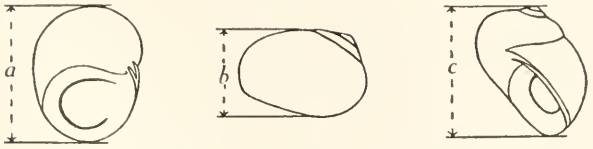

FIG. 3. Shell from Church Reef, near Plymouth, England, showing the dimensions that were measured.

(usually the overall length of the shell), the breadth (b) of the final whorl at the base of the penultimate whorl, and the distance (c) from the top of the spire to the most distant point on the lip. The ratios between these dimensions, $\frac{a}{b}$, $\frac{a}{c}$ and $\frac{c}{b}$, were calculated, and they form the basis of comparison between shells from different localities. Figure 3 shows exactly which dimensions were measured on each shell.

TABLE II

Shells from the two sides of the Atlantic: numbers of shells of different sizes.
(See Fig. 4.)

Localities	Bergen			Cattewater			Church Reef			Westerly		
Number of Shells	100			100			100			100		
Millimeters	*a*	*b*	*c*	*a*	*b*	*c*	*a*	*b*	*c*	*a*	*b*	*c*
5.75 to 6.25.....					1							
6.25 to 6.75.....					9							
6.75 to 7.25.....					28						1	
7.25 to 7.75.....					34	1					16	
7.75 to 8.25.....					13	7					43	
8.25 to 8.75.....		2			13	21					29	
8.75 to 9.25.....		25		7	2	30		5			10	
9.25 to 9.75.....		30		17		21		30			1	1
9.75 to 10.25.....		39		21	1	12		31				6
10.25 to 10.75.....		4	1	26		4		29				33
10.75 to 11.25.....			5	14		2		5		7		27
11.25 to 11.75.....			11	9		2			1	29		18
11.75 to 12.25.....	2		21	4					1	28		9
12.25 to 12.75.....	8		35	2					8	19		5
12.75 to 13.25.....	25		19				1		15	9		1
13.25 to 13.75.....	37		7				2		17	8		
13.75 to 14.25.....	19						17		33			
14.25 to 14.75.....	8		1				22		14			
14.75 to 15.25.....	1						28		9			
15.25 to 15.75.....							20		1			
15.75 to 16.25.....							7					
16.25 to 16.75.....							2					
16.75 to 17.25.....							1		1			

TABLE III

Shells from the two sides of the Atlantic: numbers of shells of different proportions. (See Fig. 5.)

Localities	Bergen			Cattewater			Church Reef			Westerly		
Number of Shells	100			100			100			100		
Proportions	$\frac{a}{b}$	$\frac{a}{c}$	$\frac{c}{b}$	$\frac{a}{b}$	$\frac{a}{c}$	$\frac{c}{b}$	$\frac{a}{b}$	$\frac{a}{c}$	$\frac{c}{b}$	$\frac{a}{b}$	$\frac{a}{c}$	$\frac{c}{b}$
0.99 to 1.03.....		4			1			3			1	
1.03 to 1.07.....		20			4			35			15	
1.07 to 1.11.....		52			17	1		47			53	
1.11 to 1.15.....		20			51	3		12			27	
1.15 to 1.19.....		4	1		21	18		3			4	
1.19 to 1.23.....			7		5	45			1			
1.23 to 1.27.....			29	1		22			2			5
1.27 to 1.31.....	1		33		1	7			5			12
1.31 to 1.35.....	7		18	15		1			21			32
1.35 to 1.39.....	38		10	45		2	3		22	1		28
1.39 to 1.43.....	27			26			6		34	13		17
1.43 to 1.47.....	21		2	12		1	26		7	24		5
1.47 to 1.51.....	5			1			31		7	36		
1.51 to 1.55.....							23		1	17		1
1.55 to 1.59.....	1						7			7		
1.59 to 1.63.....							4			1		
1.63 to 1.67.....										1		

It represents a shell from Church Reef, Wembury Bay, and the measurements in millimeters and the proportions calculated therefrom are as follows:

Length (a)	Breadth (b)	Spire to Lip (c)	$\frac{a}{b}$	$\frac{a}{c}$	$\frac{c}{b}$
16.4	10.8	15.2	1.518	1.079	1.407

SHELLS FROM THE TWO SIDES OF THE ATLANTIC OCEAN

When shells from Bergen, the Cattewater, Church Reef, and Westerly are compared, they are found to be so similar that it is impossible to separate them.

In average size of individuals the four lots vary considerably, those from the Cattewater being the smallest and those from Church Reef, only six miles away, the largest. Among the Cattewater shells, however, there were nine very large individuals illustrated by No. 6 in Fig. 6. These presumably represent a previous generation or age-group, and they have not been included in the Cattewater shells in Tables II and III and in Figs. 4 and 5. Table III and Fig. 5,

giving the numbers of shells at the different proportions, show the amount of overlap between the four lots. Bergen and Cattewater shells are very similar, and the curves for Church Reef and Westerly are well-nigh identical. The Cattewater lot are somewhat more globular than the others, but they are probably younger, if the giant shells like No. 6 are really of the mature adult size. These nine large Cattewater shells have apparently lived an exceptionally long time, for they are the largest *Littorina obtusata* in the extensive collection at Harvard, with the exception of an individual specimen from Cornwall.

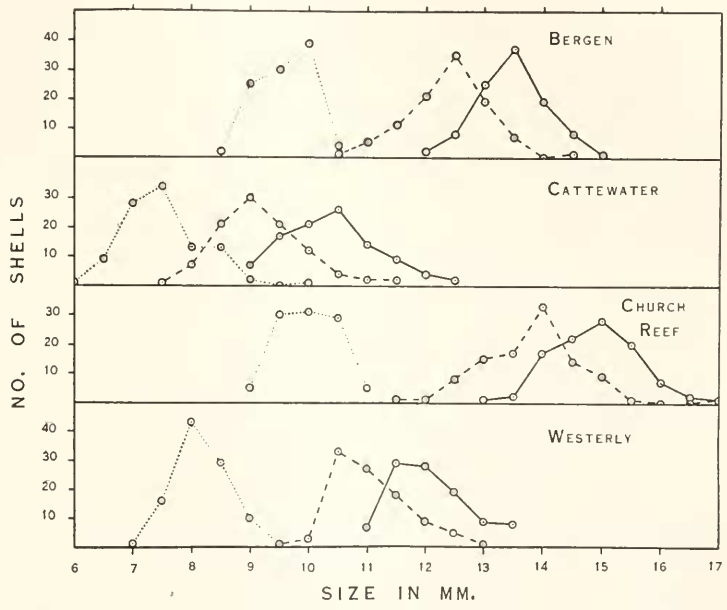

FIG. 4. Shells from the two sides of the Atlantic: numbers of shells of different sizes (See Table II). — = *a*, · · · = *b*, --- = *c*.

In Fig. 6 are shown camera lucida drawings of the obverse and reverse aspects of three shells from each locality, the relative height of the spire to the rest of the shell increasing from left to right. The dimensions and proportions of the same twelve shells are given in Table IV, where the ratio $\frac{a}{c}$ decreases in each group with the increase of the spire component, *c*.

From these figures and tables it will be seen that the amount of variation is much the same in each locality and that it would be quite impossible to sort a mixture of shells from the four places, either on

sight or after measurement. There is then no doubt of the conspecificity of *Littorina obtusata* from Bergen, from the Plymouth district and from Rhode Island.

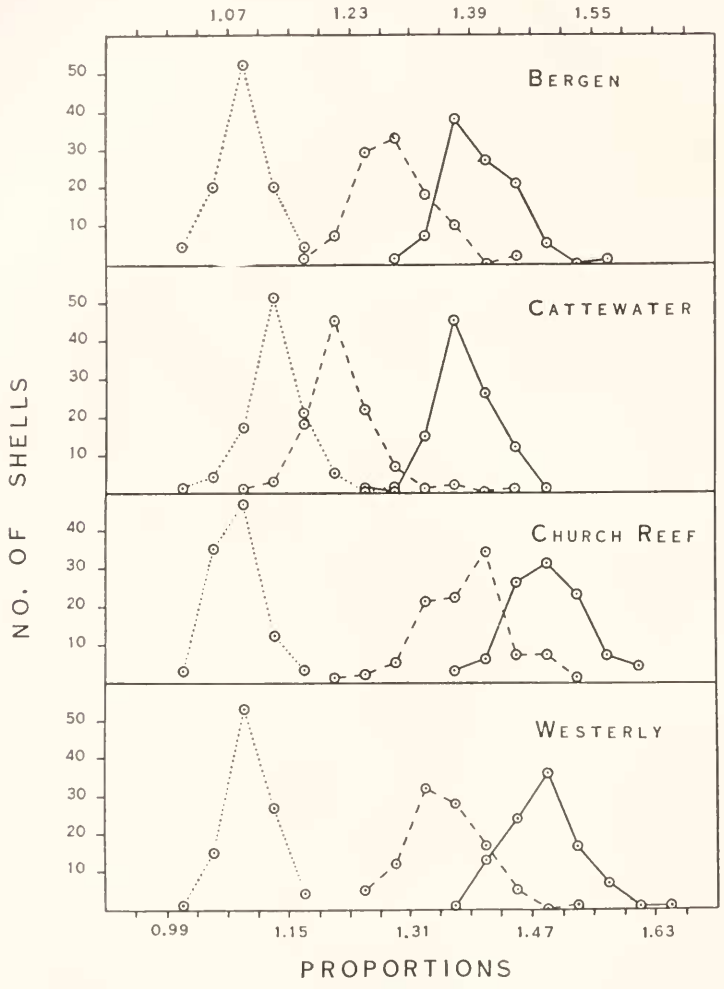

FIG. 5. Shells from the two sides of the Atlantic: numbers of shells of different proportions (See Table III). $— = \frac{a}{b}$, $\cdots = \frac{a}{c}$, $--- = \frac{c}{b}$.

SHELLS FROM THE NEW ENGLAND COAST

It has now been shown that the same species occurs on both sides of the North Atlantic. It remains to be proved that the same species extends up the American Coast, where shells called "*L. palliata*" or

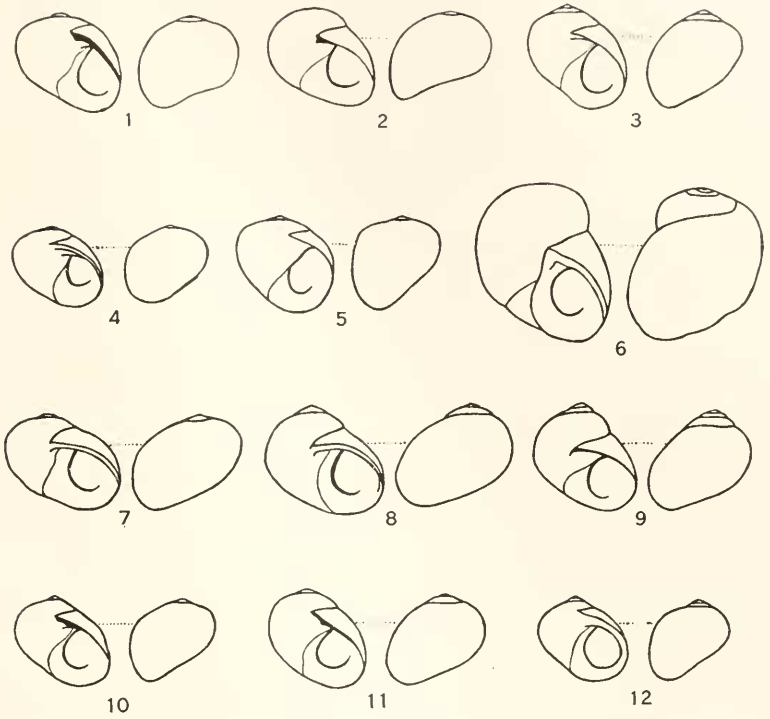

FIG. 6. Shells from the two sides of the Atlantic: obverse and reverse aspects of shells whose dimensions are given in Table IV.

TABLE IV

Shells from the two sides of the Atlantic: dimensions and proportions of shells illustrated in Fig. 6.

Locality	Length (*a*)	Breadth (*b*)	Spire to Lip (*c*)	$\frac{a}{b}$	$\frac{a}{c}$	$\frac{c}{b}$
	mm.	*mm.*	*mm.*			
1. Bergen	14.1	10.5	12.8	1.343	1.102	1.219
2. Bergen	14.1	9.9	13.0	1.424	1.085	1.313
3. Bergen	13.8	9.7	13.0	1.422	1.062	1.340
4. Cattewater	11.5	8.3	9.9	1.386	1.161	1.192
5. Cattewater	12.5	9.3	11.7	1.344	1.069	1.258
6. Cattewater	19.1	13.0	18.9	1.469	1.010	1.454
7. Church Reef	14.9	9.5	12.9	1.569	1.155	1.358
8. Church Reef	15.5	10.5	14.6	1.476	1.061	1.391
9. Church Reef	13.7	9.1	13.5	1.505	1.015	1.484
10. Westerly	12.4	8.3	11.3	1.494	1.097	1.361
11. Westerly	13.2	9.0	12.3	1.467	1.074	1.367
12. Westerly	11.2	7.9	10.5	1.418	1.067	1.329

"*L. obtusata palliata*" occur from Long Island Sound to Newfoundland.

Between shells from Westerly, R. I., and Isle au Haut, Me., there is a considerable difference, namely that between the varieties *littoralis* and *palliata* as described by Dautzenburg and Fischer (1915). These are illustrated in Fig. 7, which represents shells 10 and 33 in Table VII and Fig. 10. Without intermediate forms these might well be considered separate species, the most obvious differences being the thinner shells and the taller spires of the Maine forms. If shells from intermediate places are interpolated, however, a gradual series

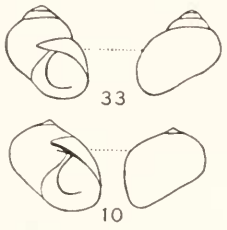

FIG. 7. Shells 10 and 33 from Fig. 10, to show the approximate limits of variation in New England shells.

is obtained between the two extremes, which makes any subdivision impossible. This is clearly shown in Fig. 9, in which the modes of the curves gradually pass from the arrangement in the Westerly lot to that from Isle au Haut, with no sudden transition anywhere. The numbers from which Figs. 8 and 9 are compiled are given in Tables V and VI respectively. In Fig. 10 are shown the obverse and reverse aspects of 24 shells, three from each New England locality, arranged as in Fig. 6 in ascending height of spire from left to right. The corresponding dimensions and proportions are given in Table VII.

Shells 10 and 11 correspond to *L. obtusata littoralis* (D. and F.), Shells 17, 18, 20 and 21 to *L. obtusata typica* (D. and F.), and Shells 29, 30, 32 and 33 to *L. obtusata palliata* (D. and F.). By Winckworth's (1922) reckoning, Shells 10 and 11 belong to a separate species, *L. littoralis*. These figures show, however, that these shells are all part of a continuous series, and any distinction into species or varieties must be purely arbitrary and taxonomically invalid.

Indeed, such bestowal of specific and varietal names and ranks on forms whose differences have not been analyzed would, if carried to the logical conclusion, necessitate the granting of a separate name to every individual (since no two are alike), with an accompanying increase in nomenclatural complexity.

TABLE V

New England shells: numbers of shells of different sizes. (See Fig. 8.)

Locality	Westerly Rhode Island			Cohasset Mass.			Briar Neck Mass.			Rye Beach N. H.			Broad Cove Maine			Port Clyde Maine			Tenants Hbr. Maine			Isle au Haut Maine		
No. of Shells	100			100			86			75			38			74			60			100		
Millimeters	*a*	*b*	*c*	*a*	*b*	*c*	*a*	*b*	*c*	*a*	*b*	*c*	*a*	*b*	*c*	*a*	*b*	*c*	*a*	*b*	*c*	*a*	*b*	*c*
5.25 to 5.75.....					3			1												10			4	
5.75 to 6.25.....					14			1			1									26			32	
6.25 to 6.75.....					38			4			1			2			2			18			50	
6.75 to 7.25.....		1			30			9			5			1			4			5			12	
7.25 to 7.75.....		16			13			16		1	12	1		11			8			1	1		2	
7.75 to 8.25.....		43			2	5		25	2		31			18			20		4		8			
8.25 to 8.75.....		29		8		16	1	20	3		21	2		3			27		9		12			2
8.75 to 9.25.....		10		16		28	2	7	5	1	4	2		3	2		13	5	14		14	6		18
9.25 to 9.75.....		1	1	19		21	4	2	5	2			2			4		1	16		14	30		18
9.75 to 10.25.....			6	25		19	6	1	12	1		5			5	2		3	11		3	37		38
10.25 to 10.75.....			33	20		9	10		16	3		12	11		10	1		5	3		6	20		18
10.75 to 11.25.....	7		27	8		2	7		18	17		21	4		9	6		9	1			6		4
11.25 to 11.75.....	29		18	4			21		5	21		23	16		7	10		14	2		2	1		2
11.75 to 12.25.....	28		9				13		12	15		8	2		3	17		14						
12.25 to 12.75.....	19		5				9		5	9		1				16		11						
12.75 to 13.25.....	9		1				8		2	4			1		1	13		9						
13.25 to 13.75.....	8						3		1	1			2		1	5		2						
13.75 to 14.25.....							3		1									1						

Table VI

New England shells: numbers of shells of different proportions. (See Fig. 9.)

Locality	Westerly Rhode Island			Cohasset Mass.			Briar Neck Mass			Rye Beach New Hampshire			Broad Cove Maine			Port Clyde Maine			Tenants Hbr. Maine			Isle au Haut Maine		
Number of Shells	100			100			86			75			38			74			60			100		
Proportions	$\frac{a}{b}$	$\frac{a}{c}$	$\frac{c}{b}$	$\frac{a}{b}$	$\frac{a}{c}$	$\frac{c}{b}$	$\frac{a}{b}$	$\frac{a}{c}$	$\frac{c}{b}$	$\frac{a}{b}$	$\frac{a}{c}$	$\frac{c}{b}$	$\frac{a}{b}$	$\frac{a}{c}$	$\frac{c}{b}$	$\frac{a}{b}$	$\frac{a}{c}$	$\frac{c}{b}$	$\frac{a}{b}$	$\frac{a}{c}$	$\frac{c}{b}$	$\frac{a}{b}$	$\frac{a}{c}$	$\frac{c}{b}$
0.87 to 0.91																							1	
0.91 to 0.95											1									1			5	
0.95 to 0.99					5									3			11			10			15	
0.99 to 1.03		1			17			5			20			16			19			18			44	
1.03 to 1.07		15			44			32			34			15			29			25			31	
1.07 to 1.11		53			33			44			18			4			15			6			2	
1.11 to 1.15		27			1			6			2												2	
1.15 to 1.19		4																1						
1.19 to 1.23																								
1.23 to 1.27			5			2			2							1								
1.27 to 1.31			12			9			10	1		8			2			2						
1.31 to 1.35			32	1		17			28			19	1		9			8			1			
1.35 to 1.39	1		28	8		21	5		28	5		24	3		12	4		15			3			2
1.39 to 1.43	13		17	24		27	21		12	24		13	17		7	7		17	2		7	2		7
1.43 to 1.47	24		5	24		11	27		6	32		7	11		5	24		14	5		18	3		11
1.47 to 1.51	36			24		8	29		1	8		3	6		2	28		10	21		14	19		17
1.51 to 1.55	17		1	8		3	4			4		1			1	8		5	20		9	20		12
1.55 to 1.59	7			8		1	1			1						1		1	10		3	20		21
1.59 to 1.63	1			3		1										1		1			2	17		12
1.63 to 1.67	1																		2		1	14		10
1.67 to 1.71																					1	4		4
1.71 to 1.75																					1	1		3
1.75 to 1.79																								1

As a final demonstration of the essential unity of *Littorina obtusata* over this considerable geographic range, embracing, as it does, both southern Norway and New England, the data of all the 933 shells from the eleven localities may be added together. This is done in

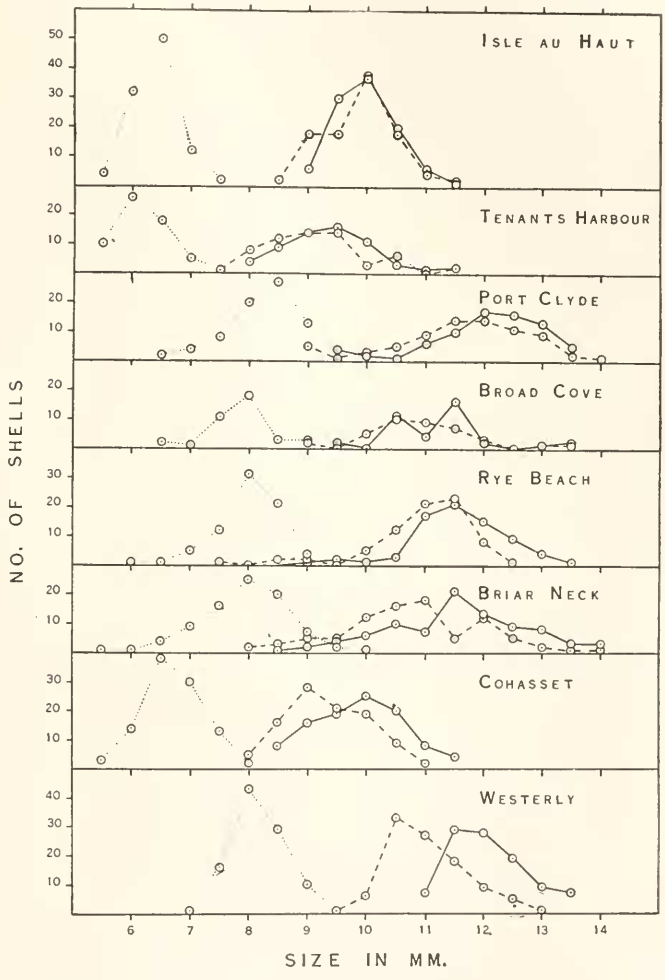

Fig. 8. New England shells: numbers of shells of different sizes (See Table V). — = *a*, ··· = *b*, --- = *c*.

Table VIII, and the result shown in Fig. 11. Although the chief distinction between so-called varieties of *L. obtusata* is usually the variation in the relative height of the spire, the curve $\frac{a}{c}$ in Fig. 11,

giving the ratio of Length to Distance from Spire to Lip, is an almost perfect frequency curve, because the series from blunt to elevated

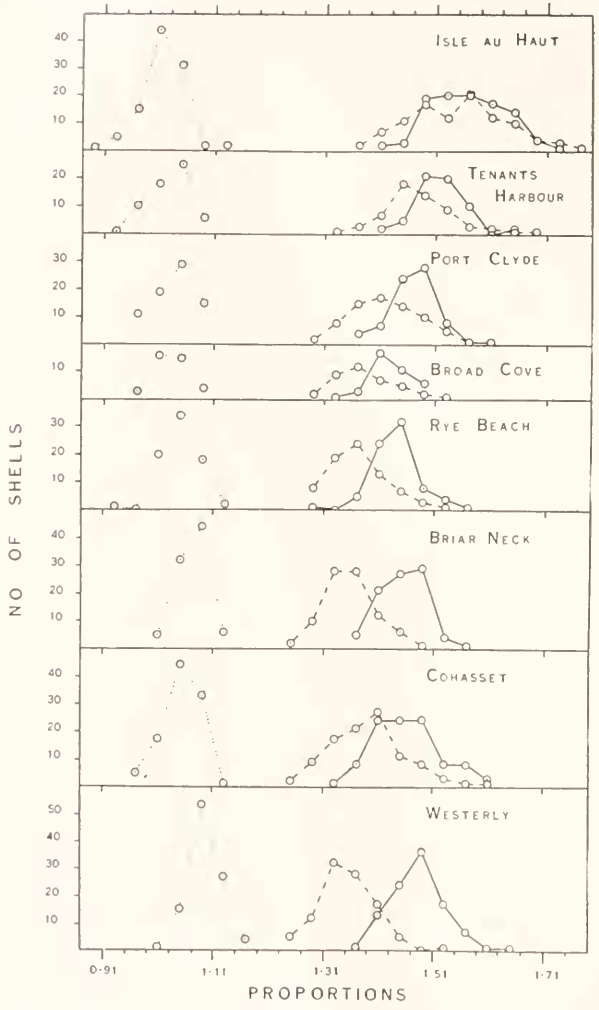

Fig. 9. New England shells: numbers of shells of different proportions (See Table VI). — $= \frac{a}{b}$, ··· $= \frac{a}{c}$, --- $= \frac{c}{b}$.

spires is continuous, with no sudden jumps. The "average" *L. obtusata*, according to these figures, will have the proportions:

$\frac{a}{b}$	$\frac{a}{c}$	$\frac{c}{b}$
1.47	1.07	1.37

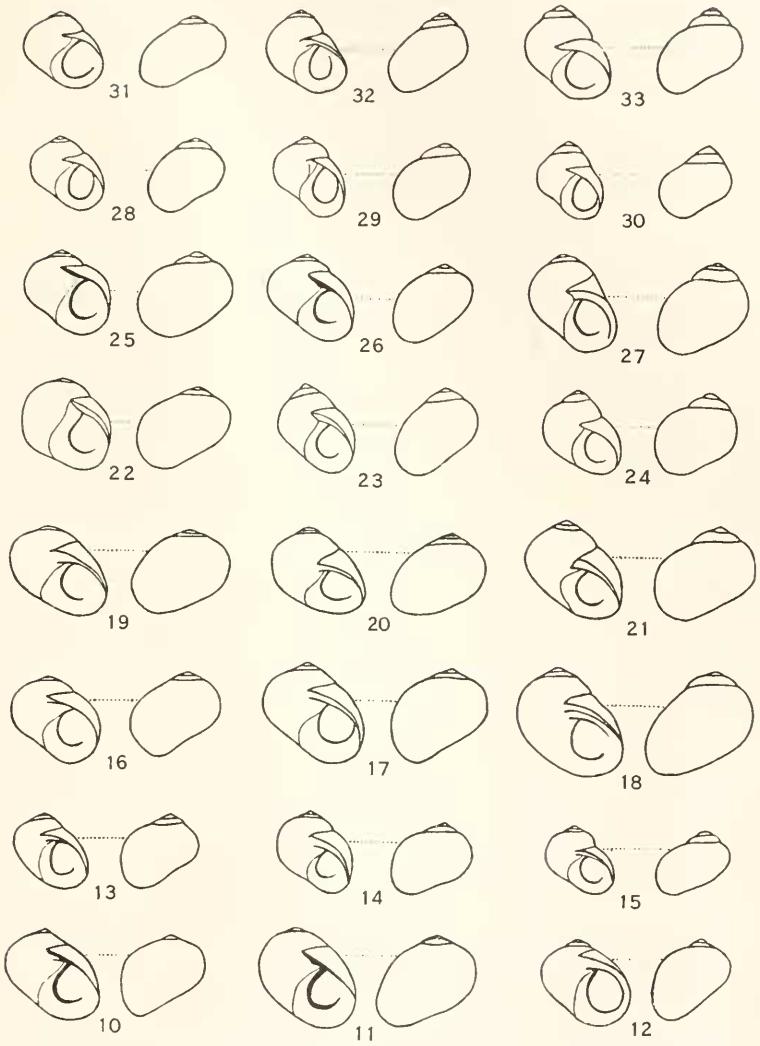

FIG. 10. New England shells: obverse and reverse aspects of shells whose dimensions are given in Table VII.

In conclusion, I wish to thank Mr. W. J. Clench, Curator of Mollusks in Harvard University, for his advice, criticism and kindness.

Table VII

New England shells: dimensions and proportions of shells illustrated in Fig. 10.

Locality	Length (a)	Breadth (b)	Spire to Lip (c)	$\frac{a}{b}$	$\frac{a}{c}$	$\frac{c}{b}$
	mm.	*mm.*	*mm.*			
10. Westerly	12.4	8.3	11.3	1.494	1.097	1.361
11. Westerly	13.2	9.0	12.3	1.467	1.074	1.367
12. Westerly	11.2	7.9	10.5	1.418	1.067	1.329
13. South Cohasset	10.4	7.0	9.8	1.486	1.059	1.400
14. South Cohasset	10.3	7.0	9.9	1.471	1.040	1.414
15. South Cohasset	9.3	6.0	9.0	1.560	1.033	1.500
16. Briar Neck	11.8	8.0	10.8	1.475	1.092	1.350
17. Briar Neck	13.0	9.0	12.4	1.444	1.048	1.378
18. Briar Neck	14.2	9.4	14.0	1.511	1.014	1.489
19. Rye Beach	12.8	8.7	11.7	1.471	1.094	1.345
20. Rye Beach	11.7	8.1	11.1	1.444	1.064	1.371
21. Rye Beach	13.0	8.5	12.4	1.530	1.048	1.459
22. Broad Cove	12.9	8.9	11.9	1.450	1.084	1.337
23. Broad Cove	11.7	8.0	11.7	1.462	1.000	1.462
24. Broad Cove	11.5	7.7	11.9	1.494	0.966	1.545
25. Port Clyde	12.4	8.5	11.5	1.459	1.078	1.353
26. Port Clyde	11.9	7.9	11.2	1.506	1.063	1.418
27. Port Clyde	12.4	8.7	12.6	1.425	0.984	1.448
28. Tenants Harbour	10.0	7.0	9.7	1.429	1.031	1.386
29. Tenants Harbour	10.2	6.9	10.2	1.479	1.000	1.479
30. Tenants Harbour	9.3	6.2	9.7	1.500	0.959	1.564
31. Isle au Haut	10.5	6.8	9.8	1.544	1.072	1.441
32. Isle au Haut	10.5	6.8	10.3	1.544	1.020	1.515
33. Isle au Haut	11.5	7.1	11.7	1.619	0.983	1.647

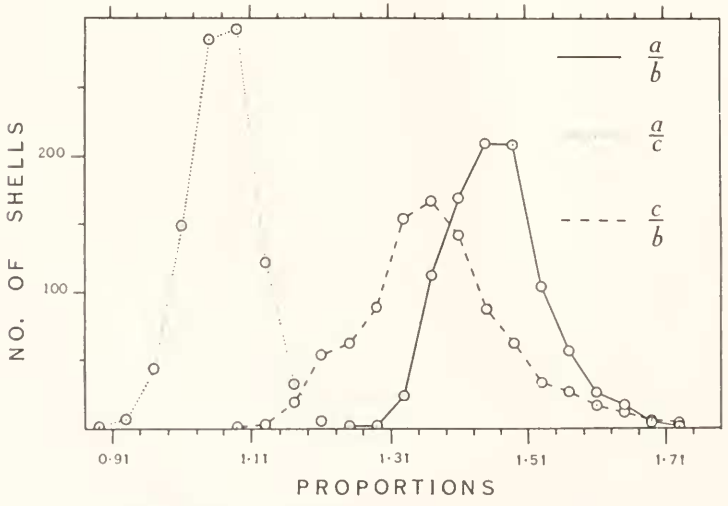

Fig. 11. Nine hundred and thirty-three shells from eleven localities on both sides of the Atlantic: numbers of shells of different proportions (See Table VIII).

TABLE VIII

Nine hundred and thirty-three shells from eleven localities on both sides of the Atlantic: numbers of shells of different proportions.

Proportions	$\frac{a}{b}$	$\frac{a}{c}$	$\frac{c}{b}$
0.87 to 0.91		1	
0.91 to 0.95		7	
0.95 to 0.99		44	
0.99 to 1.03		148	
1.03 to 1.07		284	
1.07 to 1.11		291	1
1.11 to 1.15		121	3
1.15 to 1.19		32	19
1.19 to 1.23		5	53
1.23 to 1.27	2		62
1.27 to 1.31	2	1	88
1.31 to 1.35	24		154
1.35 to 1.39	112		167
1.39 to 1.43	169		141
1.43 to 1.47	209		87
1.47 to 1.51	208		62
1.51 to 1.55	104		33
1.55 to 1.59	56		26
1.59 to 1.63	26		16
1.63 to 1.67	17		11
1.67 to 1.71	4		5
1.71 to 1.75	1		4
1.75 to 1.79			1

SUMMARY

1. *Littorina obtusata* from Norway, from the Plymouth district in England, and from Rhode Island are so alike that they cannot be separated.

2. *L. obtusata* from Rhode Island are fairly unlike those from Maine, but the examination of forms from intermediate localities establishes a continuous series up the New England coast. The range of variation remains roughly constant.

3. Further confirmation of the unity of *L. obtusata* from this wide geographical range is found by adding together the data from all the 933 shells examined. Their proportions follow almost perfect monomodal frequency curves.

4. The names *L. littoralis* (L.) and *L. palliata* (Say) must therefore go into synonymy under *L. obtusata* (L.), since it is shown that there is no division possible between forms to which these names have been given. The name *L. rudis* (Maton) must be put into synonymy,

under *L. saxatilis* (Olivi), as shown by Dautzenburg and Fischer (1912). The first definition of the genus *Littorina* is given by Férussac (1822) on p. xi of his Tabl. Syst. gén de l'emb. des moll.

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